PAPERS READ.

OBSERVATIONS ON THE FEMORAL GLAND OF *ORNITHORHYNCHUS* AND ITS SECRETION; TOGETHER WITH AN EXPERIMENTAL ENQUIRY CONCERNING ITS SUPPOSED TOXIC ACTION.

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(From the Physiological Laboratory of the University of Sydney.)

(Plates xxviii.-xxxi.)

In the year 1801 Sir Everard (then Mr.) Home examined some specimens of Platypus sent to England by Sir Joseph Banks, and remarked* as follows with regard to the spur:—

"In the male, just at the setting on of the heel, there is a strong crooked spur ½ an inch long, with a sharp point, which has a joint between it and the foot, and is capable of motion in two directions. . . . . It is probably by means of these spurs or hooks that the female is kept from withdrawing herself in the act of copulation, since they are very conveniently placed for laying hold of her body on that particular occasion."†

In 1817 an extract from a letter written by Sir John Jamieson was read to the Linnean Society of London,‡ in which, in reference to *Ornithorhynchus*, he writes:—

*A Description of the Anatomy of the *Ornithorhynchus paradoxus*. Phil. Trans. 1802, p. 72.

† Home's Comp. Anat. Vol. iii. p. 360 (1823).

‡ Note on the Venomous Nature of Wounds inflicted by the Spurs of the male Ornithorhynchus. Trans. Linn. Soc. Vol. xii. p. 584 (1818).

"The male of this wonderful animal is provided with spurs on the hind feet or legs like a cock. The spur is situated over a cyst of venomous fluid, and has a tube or cannula up its centre, through which the animal can, like a serpent, force the poison when it inflicts its wound. I wounded one with small shot, and on my overseer's taking it out of the water, it stuck its spurs into the palm and back of his right hand with such force, and retained them in with such strength, that they could not be withdrawn until it was killed. The hand instantly swelled to a prodigious bulk; and the inflammation having rapidly extended to his shoulder, he was in a few minutes threatened with locked-jaw, and exhibited all the symptoms of a person bitten by a venomous snake. The pain from the first was insupportable, and cold sweats and sickness of stomach took place so alarmingly that I found it necessary, besides the external applications of oil and vinegar, to administer large quantities of the volatile alkali with opium, which I really think preserved his life. He was obliged to keep his bed for several days, and did not recover the perfect use of his hand for nine weeks. This unexpected and extraordinary occurrence induced me to examine the spur of the animal; and on pressing it down on the leg, the fluid squirted through the tube: but for what purpose Nature has so armed these animals is as yet unknown to me."

This letter of Jamieson's induced Blainville to examine two specimens which were in the Paris Museum, and in May, 1817, he communicated the result of his observations to the Philomatic Society of Paris.*

Blainville commented on the similarity between the spurs of *Ornithorhynchus* and Cock Birds; but from their different position and connections in the Platypus, he considered it was neither a spur, a sixth toe, nor even a nail, but an apparatus peculiar to this particular animal. He described the canal of the spur, and a cyst at its base. He suggested that the latter was probably only a receptacle for poison manufactured elsewhere; but the

* Bull. Soc. Philomatique, 1817, p. 82.

imperfect state of his spirit specimens did not permit him to determine this point. He regarded the apparatus as a weapon compensating for the otherwise defenceless condition of a small animal destitute of teeth.

In 1822 Dr. Patrick Hill, of Liverpool, N.S.W., recorded* having examined a specimen which he shot. He found the spur was perforated, and had a cyst at its base. He mentioned being told by an aboriginal that a wound from the spur of the male is followed by swelling and great pain, but although his informant had seen many cases of it, he had never known it fatal.

In 1823 Home published his "Lectures on Comparative Anatomy." After describing the spur he refers to Jamieson's letter in which he narrated the finding of the canal in this structure. Home failed to find this in the first specimens he examined; subsequently however he succeeded. He says:—

"Upon examining the spur in a state of better preservation, I not only find a membranous tube passing through the spur, which has an orifice on one side near the point, but Mr. Clift succeeded, in my presence, in injecting a duct leading to a gland which lies across the back part of the thigh, over the muscles, an inch or more in length, and half an inch broad; the excretory duct passes like one ureter of the kidney, out of one side near the middle. The quicksilver injected immediately pervaded every part of the gland, and when the point of the pipe was turned downwards, ran readily to the root of the spur, where the duct made a turn, and formed a small reservoir. After a little time, however, the mucus being gently squeezed and pressed forward, we saw the mercury in the spur, and at last it came out of the orifice. When I first saw the spur, I had no doubt from its situation but that one of its purposes was to prevent the escape of the female during the act of the coitus; in this I was confirmed when I found in the female, exactly in the same situation, a regular socket, lined with strong cuticle, adapted to the reception of the spur."

* On the *Ornithorhynchus paradoxus*: its Venomous Spur and General Structure. Trans. Linn. Soc. Vol. xiii. 622 (1822).

Home, after referring to other animals as frogs, sharks, earthworms, insects, &c., which also possess accessory copulatory organs, continues as follows :—

"Having ascertained that a secretion is emitted through the spur of the male into this socket, and the parts being so minute as to require glasses of considerable power, I got Mr. Bauer to examine the socket in the female ; and after overcoming considerable difficulties, the parts being very much corrugated, and yet retaining their elasticity, he made out the form of this socket, which corresponds exactly in shape to the spur itself : so that, when completely introduced, it must be so grasped that the male would be unable to withdraw it when coitus was over ; in this respect resembling the effect of suction. The male, it would appear—at least this is the best conjecture I can make by reasoning from analogy, there being no facts to guide us by throwing some of the secretion of the gland in the thigh into the socket, dilates it, and releases the spur ; the liquor injected being acrimonious, will also irritate the female, and make her use efforts to escape."

In 1823 Meckel described* the femoral gland and its duct communicating with the spur. He showed that the cyst described by Blainville and Hill was in reality the dilatation of the duct just before entering the canal of the spur.

He afterwards (1826) published a monograph† on the anatomy of the Ornithorhynchus, in which he gives a complete account, together with several drawings, of the femoral gland and spur.

In 1824 R. Knox published an account‡ of these glands, in which, however, we have been unable to find any points of importance not treated of by Meckel.

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* Ueber den Stachel und das Giftorgan des Ornithorhynchus. Deut. Archiv für Physiol. Bd. viii.

† Descriptio anatomica Ornithorhynchi paradoxi. Lips. 1823.

‡ Observations on the Anatomy of the Duckbilled Animal of N.S.W.—the Ornithorhynchus paradoxus of Naturalists. Mem. Wernerian Soc. Nat. Hist. 1824.

In another paper* he quotes Home's theory that the spur was used during copulation, being then received into a socket in a similar position in the female.

Knox was opposed to this view of Home's, as he had found a rudimentary spur in the corresponding position in a female Echidna. It was situated in a small cavity, and of the same texture and about ¼ the size of a full grown male spur. The other parts of the poison apparatus are wanting in the female. He considered this rudimentary spur to have the same relation to the male spur, as the male breast has to the female breast.

In 1828† Thomas Axford wrote as follows :—

" It is my firm conviction that the animal has not the power of instilling poison by its spur ; and I believe this appendage is used principally for securing the female in the season of love, though it may be useful in enabling the animal to climb the steep banks of rivers. I have taken several large females, and I suppose old ones, with the hair worn off, and only a fine fur left on their rump ; and although I have killed very large males, never found one in that state. The moment I saw the first old female thus denuded, it struck me that the denudation must arise from the action of the spur of the male in holding the female. If this be the principal use of the spur, and if it contained poison, I think it would be apt to wound the female at such times. I am so convinced that the spur is harmless that I should not fear a scratch from one. However, I will try and set the matter at rest the first opportunity, by causing a male to scratch a chicken."

In 1835 Owen‡ found in young specimens of Ornithorhynchus the spur more prominent and pointed in the female, and he remarked that this is in accord with the fact that secondary sexual characters are not available for distinguishing sex before puberty.

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* Notice respecting the presence of a rudimentary spur in the female Echidna. Edin. New Phil. Journal I. 1826, p. 130.

† Edin. New Phil. Journ. vi. 1829, p. 399.

‡ On the Young of the Ornithorhynchus. Trans. Zool. Soc. Vol. i. 1835, p. 221.

In the same year (1835) Dr. G. Bennett gave an account* of a specimen he shot in September. It was wounded only, and brought in by the dog. It made no attempt to use its spur, even when handled in such a way as to enable it to readily use it if it had wished to do so. He states that the blackfellows were not afraid of handling the animal alive. He says :—"I am convinced some other use must be found for the spur than as an offensive weapon." He found a small impervious depression in the female shot on the same day, situated in a position corresponding to that of the spur in the male. There was no rudimentary spur. He thought this might serve for the reception of the spur of the male.

In 1859 the same naturalist published some observations† on two of these animals (♂, ♀) which he had kept in captivity, in which he makes the following statement :—

"From my recent observations I consider the question of the spur in the male being a poisonous weapon as now decided ; for the living male specimen, though very shy and wild, can be handled with impunity. Although making violent attempts to escape, and even giving me some severe scratches with the hind claws in its attempts, still either in or out of the water he has never attempted to use the spur as a weapon of defence."

Under the heading, "The Poison of the Platypus," the following extract is quoted in the Australian Journal of Education‡ from the "Maitland Mercury" :—"On Tuesday, the 9th instant, when Mr. E. was fishing in the river near his residence, he found that a Platypus had got entangled in the net, and upon catching the animal it immediately struck the two spurs attached to its two floats or arms into the forefinger of Mr. E.'s left hand, with such force that they penetrated through the skin and into the muscles of the finger, and it was with great difficulty that Mr. E. at last succeeded in ridding himself of his unwelcome

* Notes on the Nat. Hist. and Habits of the *Ornithorhynchus paradoxus.* Trans. Zool. Soc. Vol. i. 1835, p. 229.

† Notes on the Duck-Bill *(Ornithorhynchus anatinus).* Proc. Zool. Soc. 1859, p. 213.

‡ Aust. Journ. Educ. Sydney, 1869.

intruder and eventually killed it. Mr. E. all the time suffered intense pain, and presently the wounded finger, then the hand, and ultimately the whole arm up to the shoulder swelled to a serious extent. The symptoms usually following snake bite also set in, and after a day or two Mr. E.'s state became so serious as to alarm his friends for his safety, and Dr. G. having been sent for, he applied ammonia and the usual remedies against snake poison, and we are glad to learn that Mr. E. has now entirely recovered."

In 1876 Creighton,* writing on the Mammary Glands of Echidna and Ornithorhynchus, refers to the femoral gland in the following terms:—

"The mammary gland is found only in the female Ornithorhynchus and Echidna. But the males of Ornithorhynchus and Echidna have also a gland peculiar to them, which resembles the mamma in being a sexual gland, and in being subject to periods of expansion and functional activity from season to season. This gland is the glandula femoralis, situated on each side of the back of the thigh, and discharging by a long duct which runs down the leg and opens on the plantar aspect at the 'spur.' There is a certain probability of this gland being the homologue of the female gland, and when the very singular differences between the mammæ in the male and female Cetaceans are observed, this probability becomes much stronger. I am indebted to Prof. Flower for pointing out to me the peculiarity of the mamma in the male porpoise as shown in preparations made by himself. Instead of there being a pair of ducts, one on each side, as in the female, there is only one duct which opens by a round pore without a nipple in the middle line of the body at a point much further back than in the female. Now by those two circumstances—the singleness of the duct and its caudal position—the mamma of the male porpoise is brought within reach of comparison with the femoral gland of the male duckbill. This is nothing more than a curious suggestion; but if the

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* Journ. Anat. & Phys. Vol. xi. p. 29.

porpoise be represented with a pair of hind limbs, the single duct of the male mamma opening in the middle line far back on the ventral surface would then be represented by a pair of ducts going with the limbs, and that is exactly the condition in the male duckbill."

In 1876 Spicer communicated an account* of injurious effects following wounds made by a Platypus with its spurs in the hand of a friend of his. This account corroborates in every particular those previously mentioned in this paper. Mr. Spicer points out the difference between the effects in the above-mentioned case and the usual effects of lacerated wounds, and considers that the small, non-lacerated wound, the rapidity with which the symptoms follow, and their intensity indicate more than can be accounted for by a mere wound. He instances the relationship of Saurians and Ophidians to Monotremes as indicating the possible family right of the latter to the possession of a poison apparatus; but remarks that its existence in the male alone is unusual, since in cases where such is found in one sex only—as in some insects—it is usually the female which exhibits it. He refers to the seasonal variation of snake venom, and states that "its virulence depends largely on the circumstances under which it is received." He quotes the opinions of Bennett and Owen with regard to the sexual nature of the gland, and considers it possible that during the pairing season (the time of the year when the above-mentioned case occurred) the secretion "may have some peculiarly acrid or irritant property, and when injected into the human body may produce similar symptoms to those of a true poison." He also quotes Baden Powell ("New Homes for the Old Country"), who thinks that when no harm results from Platypus wounds, it is perhaps because the poison sac is empty at the time, or that the animal does not use the spur when on land (out of its proper element). Baden Powell further suggests that the spur and secretion may be used for toilet purposes, the animal being known

* On the Effects of Wounds inflicted by the Spurs of the Platypus. Papers and Proc. Roy. Soc. Tasmania, 1876, p. 162.

to clean itself with its hind legs. Mr. Spicer thought such a usurpation by the male of feminine privileges would be as singular as the animal's taste in hair oils.

A Nicols* records having wounded and captured a Platypus which was lively enough to scratch him with its sharp claws, but made no attempt to use its spurs when handled. The native who accompanied him, however, expressed fear of the spur. Nicols thought that the spur and its gland might be "a remnant of conditions of life very different from those under which the animal now exists." He considered that although it might possibly be used in contests with its own kind, "there is no reason for attributing a poisonous character to this weapon."

Darwin (Descent of Man, 2nd ed. p. 502), when discussing the weapons of offence possessed by the males of various kinds of animals, mentions the spur and gland apparatus, but states that Harting has shown that the secretion is not poisonous.

In his recent Presidential Address to the Royal Society of N.S.W., Prof. Anderson Stuart† refers to the cases recorded by Jamieson and Spicer, and gives an account of the effects of the poison on dogs. One of these animals received the wounds whilst retrieving. Their infliction was rapidly followed by great swelling of the face, which was very tender. The dog became sleepy, and refused food. He had no salivation, vomiting, diarrhœa, tremor, convulsions nor staggering. He ultimately recovered.

Another Platypus hunter stated that he had lost in this way four valuable dogs of comparatively large size. On one occasion he "saw the Platypus strike, heard the dog whine, saw the wound, and the train of symptoms ending in death." In these cases the most marked constitutional effect was intense drowsiness.

In summing up on the question, Prof. Anderson Stuart says:— "We may, I think, conclude that the poison is powerful enough, at all events at certain seasons, but at what seasons the accounts

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* Zoological Notes. London, 1883. Chap iv. p. 116.

† Royal Soc. of N.S.W. Anniversary Address by the President, Prof. T. P. Anderson Stuart, M.D., 1894.

do not permit me to say, though I think it is the pairing season. I have set down these new accounts because I believe them worthy of record, and perhaps this allusion may lead to something more being done."

Still more recently other cases (two men and two dogs), displaying severe symptoms following wounds from the spurs of these animals, have been recorded by Dr. Lalor in a communication to the Victorian Branch of the British Medical Association.*

We are unacquainted with Dr. Lalor's paper, but from the abstract we have seen, the principal symptoms appear to have been great œdema and rise of temperature. In one case, that of a man, the temperature rose to 104° F.

From the above historical summary one sees that four views have been entertained concerning the function of these glands and their associated spurs, viz. :—

(1) That they are in some way accessory to the organs of generation (Home, Bennett, &c.).

(2) That they are poison glands, and as such constitute important weapons of offence (Jamieson, Blainville, Hill, Meckel, Knox, Spicer, &c.).

(3) That the secretion is used for toilet purposes (Baden Powell).

(4) That they are a remnant of conditions of life very different from those under which the animal now exists (Nicols).

We will consider the last suggestion first. This, while it is very difficult to show that it is false, does not appear to us very reasonable. It would be highly improbable that a complicated arrangement such as we are considering should be retained in such a condition of functional perfection if it were of no service to the individual or the species.

Baden Powell's notion that it may be used for toilet purposes is unlikely. Spicer pointed out that it was confined to the male sex, and Bennett observed that the specimens he had in his

* B.M.J. June 16th, 1894, p. 1332 (abstract of paper).

possession never used their spurs for this purpose, but smoothed their locks by using their claws as a comb. From its position also it is unsuited for such a purpose.

Home's suggestion, which had the powerful support of Dr. Bennett, cannot be absolutely denied, as no one has, as far as we are aware, ever seen these animals copulating. Home's main reason for such an hypothesis was that in the female there are situated in corresponding situations slight hairless depressions.

It seems to us that for the male to apply its spurs to these depressions during copulation in the manner suggested by Home would involve an amount of gymnastic ability of which even an Ornithorhynchus is incapable.

Moreover, Knox* and Owen* have shown that these depressions in the female are merely the rudiments of the male spur, and that the young female, indeed, actually possesses a spur which disappears prior to the dawn of sexual life.

Bennett did not espouse Home's theory very strongly, but having come to the conclusion that the poison hypothesis must be discarded, put forward, as a possible explânation, the suggestion that the spurs play the same part in fixing the female as the appendages of some Crustaceans and other lower animals.

The only remaining theory, that the whole apparatus forms a powerful weapon of offence (at any rate at certain periods) has a large number of facts to support it. We have the above-mentioned well authenticated cases of serious results following a wound by the spur; not to mention any amount of native tradition. As has so often been pointed out, the train of symptoms following such wounds are absolutely unlike those produced by a simple puncture or by the introduction of septic material. The almost immediate and lasting depression, the intense pain, and great œdema and absence of suppuration have led more than one observer to compare the result with that produced by snake poison. Moreover, a precisely similar train of symptoms presented themselves in every case, whether in man or animals.

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* *Loc. cit.*

In the accounts of those naturalists (Bennett, Nicols and others) who have thought the spur was not used as a weapon of offence, it is invariably stated that the animals handled by them made no attempt to use their spurs. They do not instance any cases in which wounds were made without injurious results.

This negative evidence is of little value compared to the cases quoted above. Taking all these facts into consideration, it is at least difficult to avoid the conclusion that the gland and spur constitute a weapon of offence.

Quite recently we were fortunate enough to receive, through the kindness of Dr. G. Elliott Smith, a supply of material in very fair condition for ordinary anatomical and histological investigation. At the same time Dr. Smith obtained for us a small amount of the secretion of the glands. In addition to this, we have had the use of some preserved specimens kindly placed at our disposal by Prof. Wilson. We wish here to acknowledge our indebtedness and express our thanks to these two gentlemen.

The naked eye anatomy and anatomical relations of the femoral gland and its duct and spur have been so well described by Meckel* and Owen† that we feel we have little further to add. In view of the fact, however, that these descriptions were written from the dissection of preserved specimens, we have deemed it advisable to risk repetition by giving a short account of it here.

Anatomy of the Glands.

The femoral or crural glands (Pl. XXVIII. *i*) are two whitish bodies shaped somewhat like a cocked hat, situated symmetrically one on each side of the spine over the acetabulum and femur. They are covered by skin, panniculus carnosus, and deep fascia, the latter forming a special compartment in which the gland lies. At the inner side of each, and slightly overlapping part of the inner border, is the gluteus maximus muscle; at the outer

* Desc. anat. Ornithor. paradox.

† Todd's Cyclopædia, Art. Monotremes.

side are the muscles of the leg. Anteriorly it reaches the border of the obliquus externus abdominis muscle and posteriorly touches the biceps, under which its duct passes. From above downwards it rests on the rectus, iliacus, gluteus minimus and g. medius muscles.

A gland of average size measured 3 cm. in length, 2 cm. in breadth at its widest part, and about 1·5 cm. in thickness. The outline is somewhat reniform, the inner border being strongly convex, and the outer marked by a deep indentation about its middle, somewhat resembling the hilus of a kidney. The ends are rounded; the anterior is larger and thicker and is directed outwards; the posterior is smaller and thinner, and directed backwards. It is flattened dorso-ventrally, the dorsal surface being slightly convex and the ventral flatter. The surfaces show the lobular character of the gland. From the posterior half of the outer border the duct emerges, and passes downwards, with the nerves and vessels, on the posterior aspect of the leg. It is about 5 cm. in average length, and in an undilated state about 2 mm. in external diameter. After leaving the gland it passes down under the biceps muscle, internally to the tendons of the tibialis posticus and flexor longus hallucis muscles, then crossing obliquely the tendon of the gastrocnemius, reaches the base of the spur. Here it becomes dilated into a sac which is so deeply embedded in the ligamentous tissue at the back of the tarsus that its isolation is a matter of difficulty. From this dilatation a prolongation extends into the canal in the spur. (Pl. XXVIII.)

The nature of the spur has already been sufficiently well indicated. It is attached to a supernumerary tarsal ossicle which is articulated to the astragalus and tibia. The powerful gluteus maximus is inserted at the base of the spur, and is in all probability the muscle brought into action when the animal "strikes."

Histology of the Gland and Duct.

The minute structure of the gland and duct was studied in specimens from three adult individuals shot near Raymond Terrace, N.S.W., on June 6th, 1894. They had been placed in

92% alcohol two days after the animals were killed. The weather at the time was cold, so that the tissues were in very moderate condition notwithstanding this delay. Transverse sections of these were cut from pieces embedded in paraffin and also in gum. The sections were stained in hæmatoxylin and borax carmine.

The gland is of the compound racemose type. The duct, traced into the gland, divides repeatedly into smaller and smaller branches—the final branches opening into the alveoli. Each gland is divided into lobules (Pl. XXIX. figs. 1 and 2), all of which show numerous alveoli and ducts in a connective tissue stroma. The alveoli are dilated, and lined by a single layer of epithelial cells situated on a basement membrane.

The epithelial cells (Pl. XXX. fig. 1 *a*) are large, irregular in shape, and have flattened nuclei at the deeper part of the cell. The nucleus and that part of the protoplasm nearest the attached end of the cell take the stains readily. The rest of the cell is occupied by coarsely granular material which did not stain with nuclear stains. This appearance corresponds to the condition observed in the cells of a mucous salivary gland prior to the discharge of its secretion. The portions of the ducts seen in the sections (viz., the portions within the gland), are lined by a single layer of large columnar cells seated on a basement membrane.

The stroma (Pl. XXX. fig. 1 *b*) presents the usual characters of white fibrous tissue. It is formed by the septa passing in from the fibrous layer of the capsule which divides the gland into lobules.

The capsule consists of two coats:—

(1) The fibrous one just alluded to (Pl. XXX. fig. 1 *c*), consisting like the stroma of white fibrous tissue, and containing a liberal supply of blood-vessels and nerves.

(2) A layer of unstriped muscular tissue, three or four cells deep, situated outside the fibrous coat (Pl. XXX. fig. 1 *d*).

Outside of these is the investment of fibrous tissue derived from the deep fascia, which is not shown in the drawings, having been removed in the process of dissecting out the glands.

The layer of smooth muscle fibres is no doubt brought into action to help to express the secretion when the animal "strikes." The large alveolar spaces as well as the duct serve as store-house for this fluid. When the animal contracts its powerful gluteus maximus and the other muscles at the back of the thigh, the gland would be compressed to some extent. As, however, these muscles must be constantly so contracted when the animal runs and swims without causing the discharge of the contents of the gland, such muscular contraction cannot be considered as the only cause operating. We think that the contraction of the thick panniculus, which envelopes the leg in this region, is in all probability the principal agent concerned, and that the smooth muscle of the capsule co-operates with it in effecting this end. The fact that the muscle fibres of the gland itself are of the unstriped variety, does not necessarily prevent them from being indirectly under the influence of the will. The pupil of the eye in mammals is provided with muscle of the same unstriped character, which can be brought into operation in associated action with certain voluntary muscles.

As regards the duct proper, sections were made from a portion about midway between the gland and spur. Most of these (Pl. XXIX. fig. 3) showed two channels (some, however, three and others only one) embedded in white fibrous tissue. This duplication of the lumen of the duct, which was noted by Rudolphi,* indicates that in the development of these specimens the branching of the original invagination had occurred lower down than is usual in such structures. In all cases the duct was single at the lower end. The duct contains no muscular tissue whatever. We have made serial sections from every region, including the dilatation situated at its lowest end, without discovering any trace of muscle. This seems to us the more remarkable as under ordinary circumstances it is impossible, either in the living or recently dead animal, by pressing on the gland to drive the secretion through the spur. So that the animal must possess some arrangement for obliterating the channel and so preventing undue waste of the secretion.

* Abhand. d. Berlin. Akad. 1820-21. Abtheil. i. p. 233-236.

Each of the channels is lined by four layers of epithelial cells situated on a basement membrane. Those nearest the basement membrane have large oval nuclei, and are arranged round the duct with their long axes parallel to the basement membrane on which they rest. The innermost layer consists of irregularly pear-shaped cells, with elongated nuclei arranged radially, their larger ends towards the duct of which they form the immediate lining. Between these there is a layer one or two cells deep—the cells being of an irregular rounded form and having rounded nuclei.

Sections of the saccular dilatation at the base of the spur showed similar characters to those of the duct just described, but the enclosed cavity was much larger. No muscular tissue was noted, and from the manner in which this sac is embedded in dense ligamentous tissue, muscular fibre would be of little use in this situation.

When we compared the sections obtained from these specimens with some previously obtained by one of us (M) from a fresh specimen killed in April, 1892, at Wellington, N.S.W., we noticed a very marked difference in the minute structure of the gland and in the character of the cells lining the alveoli (*cf.* Pl. XXIX. figs. 1-2, and Pl. XXX. figs. 1-2).

(1) The proportion of fibrous tissue to gland structure proper was very much greater in the latter.

(2) The alveoli also were very much smaller, and the duct leading from each alveolus, instead of being lined by columnar epithelium, showed four layers of cells as in the larger duct which delivers the poison to the spur as above described.

(3) In the latter specimen the glandular epithelial cells were smaller and more regularly cubical in shape. Their nuclei were rounded and in the middle of the cell, and they and the protoplasm stained readily throughout. The protoplasm was moreover only finely granular.

This appearance forms a marked contrast to the large elongated, coarsely granular cells, with their nuclei pushed to the attached end of the cell, which we found in our second specimens killed June 6th. The variations in structure between these two glands recall to one's mind the differences between an actively secreting mammary gland and one which has undergone retrogressive metamorphosis.

It is interesting to note that corresponding to these differences in minute structure, differences in the physiological action of the secretion obtained from them were observed.

The secretion from the first described glands in which the cells were in an "active" condition produced a marked poisonous effect when injected into rabbits, whilst that from the second gave negative results.

Note on the Chemical Composition of the Secretion.

This and the following portion of this paper dealing with the toxic action of the secretion of these glands, must, in consideration of the small amount of material at our disposal, be looked upon merely as a preliminary communication. But as we cannot tell how long it may be before we are fortunate enough to obtain further supplies, and considering the very definite nature of our results, it seems quite worth while to publish them at the present time.

More than two years ago one of us (M.) attacked this subject. A pair of glands (fresh) which were supplied through the kindness of Prof. Wilson, were chopped up and extracted with dilute salt solution, and the nature of the extract examined. This examination showed that in addition to the albumins, globulins and nucleo-albumins, which might be extracted by such treatment, there was present in the extract a small quantity of proteose.

The innoculation experiments, however, both with the first extract, and with the separated proteose, gave negative results.

As the poisonous constituents of snake venom had been shown* to be due to proteoses, and in the light of the above results, we

* Weir Mitchell, Smithsonian Contrib. to Knowledge, 1886. Wolfenden, Jour. Physiol. Vol. vii. ; Kaulback, *ibid.* Vol. xiii. Martin and Smith, Proc. Roy. Soc. N.S.W. 1892.

considered it extremely probable that the toxic properties, if any, of the glands might be due to proteoses (albumoses) also. We accordingly requested our friend Dr. G. Elliott Smith, who had heard of the slaughter of some Platypi by a friend of his up country, to express the contents of the ducts and glands into a bottle of strong alcohol, whereby all the albuminous constituents would be precipitated. This Dr. Smith very kindly did for us. The glands and ducts were carefully dissected out and a ligature applied to the periperal end of each duct, and the whole removed. The ducts, which were distended with secretion, were then cut just above the ligature, and by gentle pressure the larger alveoli of the glands and the ducts were emptied of their secretion.

Three pairs of glands were treated in this way, the liquid expressed being limpid and opalescent. The strength of the alcohol used was 92%. We received the bottle containing the alcohol and precipitated secretion four days later. The precipitate was separated from the alcohol by filtration and dried at 40° C. and powdered. We obtained in this way a little less than ·4 gramme of a pearly white powder, which was in large part soluble in water and dilute saline solutions, forming a slightly opalescent liquid.

This solution, which we found to contain the active substance of the secretion, was neutral in reaction and behaved in the following manner with reagents :—

(1) Warming with nitric acid and subsequent addition of ammonia – orange colouration (xanthoproteic reaction).

(2) On addition of Millon's reagent, it gave the usual proteid reaction.

(3) Heating (after previous acidulation with acetic acid) produced a turbidity between 75° and 80° C. At about 80° C. a considerable flocculent precipitate came down. This was filtered off, and the filtrate found to still contain a small quantity of proteid, as it gave a biuret reaction.

(4) With caustic potash and a trace of copper sulphate a violet biuret reaction was obtained.

(5) Nitric acid produced a precipitate which was not appreciably diminished by warming.

(6) Picric acid produced a precipitate which was not appreciably diminished by warming.

(7) Acetic acid produced no turbidity.

(8) Saturation with magnesium sulphate did not produce any precipitate.

(9) Saturation with ammonium sulphate produced a precipitate. This was filtered off and the filtrate contained no proteid.

From the above it is obvious that there were at least two proteids present in our original solution—

(1) A proteid coagulated by heat.

(2) A proteid soluble at 100° C.

The former appears from the above reactions to belong to the albumen class, as the presence of nucleo-albumen (nucleo-proteid, Hammarsten) was excluded by the absence of any precipitate of nuclein on submitting the clear solution of the proteid in 2% HCl to peptic digestion for some hours (12) at 37° C. The albumen, however, had undergone digestion and had been converted into deutero-proteose and peptone, for the solution now reacted in the following manner:—

(1) Boiling acidulated solution. No precipitate.

(2) KHO + $CuSO_4$. Strong *pink* biuret reaction.

(3) HNO_3. No precipitate, but on further addition of NaCl turbidity which disappeared on heating and returned on cooling the solution.

(4) Saturation with $Am_2 SO_4$. Slight precipitate. Filtrate contained peptone.

To determine the nature of the proteid present in the filtrate after precipitation by heat, we boiled some of the solution which had been previously acidified with acetic acid, and separated the heat precipitate by filtration. An equal volume of trichloracetic acid was added to the filtrate. This caused a slight turbidity, which, however, disappeared on heating the solution, but reappeared directly it was allowed to cool.

It was filtered boiling through a funnel surrounded by a hot water jacket. The filtrate became slightly milky on cooling, and when rendered alkaline with strong caustic potash and a few drops of copper sulphate added, showed a pink biuret reaction.

By this treatment the presence of a very small quantity of proteose may be demonstrated when such is present together with ordinary proteid.*

Our conclusions as to the composition of the secretion drawn from the above experiments are:—

(1) It is a solution of proteids.

(2) That the greater portion is composed of a proteid belonging to the class of albumins, and that in addition a small quantity of proteose is present.

(3) Nucleo-albumens are absent.

The minor portion of proteid which is rendered permanently insoluble by alcohol may contain globulin, but none of this proteid went into solution subsequently.†

As we shall show in the next section, the secretion of these glands is capable of exerting a powerful toxic action on rabbits. Whether the whole of the proteids contained possess this power, or whether it is confined to the small quantity of proteose present, we are unable to state. There would, however, be no great difficulty in answering this question had we more material to work upon.

Experiments on Rabbits with the Secretion.

The small amount of the secretion in our possession necessarily limited the number of experiments on the nature of its toxic action. We were, however, able to make four experiments, the

* C. J. Martin, Journ. of Physiol. Vol. xv. p. 375.

† That a body of the albumen class, after four days' sojourn under 92 % alcohol, should readily dissolve in water and dilute saline solutions is peculiar. Ordinary albumens, including the serum-albumen of the Platypus itself, are in this length of time rendered insoluble.

results of which were sufficiently definite. Rabbits were chosen for the purpose, on account of their suitable size.

The following are the details :—

Experiment I: On June 18th, 1894, a healthy rabbit of average size and in a very lively condition had ·05 gramme of the poison dissolved in 5 cc. of 75% salt solution injected under the skin of the abdomen at 2 p.m. Its temperature at the time was 102° F. During the injection the animal struggled, and afterwards remained much quieter. For the rest of the day the animal remained very quiet in its cage, but no local signs were observed.

June 19th. A swelling about the size of a duck's egg has appeared near the seat of injection. This swelling has a semi-cystic feel, is not circumscribed, is movable over subjacent tissues, but adherent to skin. It is tender to the touch. The animal is sick—it does not struggle nor attempt to escape when handled, its eye is dull, and it eats only sparingly. Temperature 102·8° F. A specimen of blood removed from the ear clotted readily in a few minutes, and was normal in microscopic appearance. At 6 p.m. the same day the swelling had slightly increased, extending upwards over thorax. The animal has been quiet all day, remaining huddled up in a corner of its cage, and passively submitting to handling. Temperature 103·1° F.

June 20th. The swelling is much smaller and is less tender. The animal is much livelier, has taken more food. Temperature 102·8° F.

June 21st. The swelling has almost disappeared. The animal is very lively, taking food well, and struggling when handled. Temperature 102·6° F.

June 22nd. The swelling has quite disappeared; the eye is bright and the animal apparently quite recovered. The seat of injection has a bruised appearance, but is not tender to the touch. After this no further symptoms appeared; the animal recovered completely from its illness in five or six days after the injection. It is at the present time (July 28th) alive and well.

Experiment II: A rabbit about 3 lbs. in weight was etherized and cannulæ inserted into the left jugular vein and carotid artery, and a small sharp pointed cannula was passed through the wall of the trachea. The cannula in the trachea was connected by a piece of rubber tube with a small tambour, covered with thin india-rubber sheeting. The movements of the india-rubber were transmitted to a lever, the end of which marked by means of a writing point, on a travelling surface of smoked glazed paper. As the animal sucked in air with each inspiration, the rubber was pulled down and the lever marked a downward stroke on the paper. When air was expelled with each expiration the rubber membrane rose and the lever described an upward stroke. In this way a record showing the extent, frequency and general character of the respiration was obtained. The interior of the artery was connected with a mercury manometer, the movements of the mercury in the distal limb of which were recorded on the paper by means of a light float and stile carrying a writing point. In this manner a record was obtained of the pressure of the blood exerted upon the walls of the vessel (aorta), as well as every variation of this pressure due to the heart's pumping fresh quantities of blood into the aorta at each beat, and to the respiratory movements of the animal.

In addition to these records, the time was marked by an electromagnet in connection with a clock, so that at each second a small vertical line was drawn. The exact movement at which the injection was commenced and ended was also indicated by another writing stile, which described a horizontal line on the travelling surface.

During the injection this stile which was connected with an electromagnet, was raised by closing the circuit and fell again at the termination of the injection when the circuit was opened, by its own weight. In this way the duration of the injection was indicated by raising this horizontal line. The writing points of all four records were previously carefully adjusted so as to register exactly in the same vertical line.

The cannula in the external jugular vein was used to introduce the solution of the gland-secretion. This was dissolved in a ·75% solution of common salt, and was of such strength that 1 ccm. contained 0·01 gramme of our dried secretion. Having started our smoked paper travelling, and arranged the respiratory and blood pressure records, we first allowed the apparatus to run in order to obtain a portion of record previous to the introduction of the solution. Of the solution 6 ccm. (= 0·06 gramme) were then rapidly introduced through the external jugular vein.

Within three seconds from the commencement of the injection, the blood pressure, which was previously equal to 97 mm. of mercury, fell almost vertically to 60 mm. (mercury), when the heart beats were seen to become much less frequent. At the same time the respiration became hurried and exaggerated, and speedily terminated in a series of expiratory convulsions. The appearance was exactly the same as if one had clamped the wind pipe and so asphyxiated the animal—only much more rapid in its onset. During this convulsive period the blood pressure rose again, even higher than before the injection, but speedily fell again to within 27 mm. of the abscissa. By this time—90 secs. from the time of injection of the solution—the records of the heart's beats disappeared from the tracing and the respiration had ceased. A post mortem examination was immediately made. The heart was still beating feebly and continued so to do when removed from the body. The right chambers of the heart, and the whole of the venous system were discovered to be full of clotted blood. The left cavities of the heart and the pulmonary veins contained fluid blood, and there was an extensive subendocardial hæmorrhage in the left ventricle. This result might perhaps have puzzled us had we not had numerous opportunities of witnessing precisely the same results after the introduction of the venom of the Australian black snake or tiger snake* into the veins of dogs and rabbits.

* C. J. Martin. "On some effects upon the blood produced by the injection of the Australian black snake." Journ. of Physiology, Vol. xv. No. 4, 1893.

Almost immediately after the injection of the solution, more or less extensive clotting of the venous side of the heart and great vessels had taken place, and the circulation of the blood had very soon been brought to a standstill. The dyspnoeic convulsions followed from the consequent deprivation of the nervous system of oxygen.

As mentioned previously, at death the blood pressure in the arteries did not fall as is usual to within a few mm. of the zero line, but remained considerably above this (27 mm.). The explanation of this is that owing to the extensive solidification of the blood, the arteries were unable to empty their contents into the veins.

Experiment III: A rabbit of 3 lbs. weight was etherized and prepared in exactly the same manner as described in Experiment ii. In this case 4 ccm. of a 1% solution (= 0·4 gramme) of the secretion were very slowly injected into the jugular vein. The blood pressure at the moment of injection was equal to 138 mm. mercury. It fell in five seconds to 76 mm., and by the end of the injection, which lasted 40 secs., was only 42 mm., *i.e.*, less than one-third of its previous height. The heart at the same time became much slower and feebler in its action.

At the end of half an hour the pressure was only 20 mm., and the heart was beating very feebly. At this point a further injection of 4 ccm. of the same solution was introduced. This was immediately followed by asphyxial convulsions and death. On opening the body, the whole of the venous system and right cavities of the heart contained solid blood, so that on cutting across the large veins not a drop of blood flowed out. The aorta and other large arteries also contained clots. The examination was made immediately, the heart continuing to beat feebly for some minutes after removal from the body. The left ventricle showed hæmorrhages under the endocardium as in Experiment i.

Experiment IV: In this experiment we tried the effect of a much smaller dose of the secretion. Everything was arranged as in Experiments ii and iii. The same solution of the secretion was used (viz., a 1% solution in ·75% salt solution).

The blood pressure previous to the introduction of the solution was equal to 108 mm. mercury; the heart beats were 300 per minute and the respirations 48 per minute. Of the solution 2cc. were then introduced (·02 gramme secretion).

The blood pressure fell suddenly to 55 mm., the heart beats to 228 per minute (Pl. XXXI.). The respirations were not altered in frequency, but became slightly irregular. For 90 seconds the blood pressure continued to fall steadily, notwithstanding the heart's beats soon reached 300 per minute again; they were, however, much enfeebled. At the end of that time, the pressure was 46 mm. A further dose of ·02 gramme was then injected. There was a very slight further fall of blood pressure (to 42 mm.) and the heart's beats became reduced to 228 per minute again, the respirations also becoming irregular.

From this time the fall in blood pressure was steeper (as marked by the curve), so that at the end of $2\frac{1}{2}$ minutes from the commencement of the experiment it was only equal to 26 mm. of mercury. The heart's beats had by this time become practically obliterated on the tracing, although the heart could still be felt feebly beating.

During this time the respirations had become irregular both in frequency and depth, and gradually becoming weaker and weaker, were finally reduced to occasional inspiratory gasps.

In 26 minutes from the beginning of the experiment the animal quietly died.

A post mortem examination revealed nothing except hæmorrhages under the endocardium of the left ventricle of the heart. The blood was not clotted in any of the vessels, and on being drawn off coagulated much more slowly than normally, taking 12 minutes.

These four experiments prove that the secretion of the crural gland contains some body which is capable of exerting very considerable toxic action when introduced into the body of rabbits. In the section of this paper devoted to the consideration of the composition of the secretion, we adduced evidence that it contained proteids, and we have just seen that the introduction of these proteids into the animal economy may lead to fatal results.

The possibility that the toxic agent may be of other than proteid nature, but inseparable from the proteid constituents by the means employed, must remain open. The small quantity of the secretion at our disposal (less than ·4 gramme) did not admit of any varied or extensive methods of purification. We do not, however, think that such is the case, as we have knowledge of other proteids which are capable of producing similar results to those obtained.

The close analogy between some of the symptoms observed by us and those recorded as occurring in men and dogs when poisoned by wounds from the spur, lead us to expect that had we used other animals for our experiments, the results would have been parallel.

In Experiment i, in which the poison was introduced subcutaneously, the symptoms were precisely similar to those exhibited after wounds from the spurs, in which the secretion would almost certainly be injected under the skin.

In the other experiments in which the secretion was intra venously injected, the conditions were so different that they are not comparable to the same extent.

The most striking effect is, perhaps, the almost universal thrombosis which occurred in those experiments in which the poison was rapidly introduced directly into the circulation (Exps. ii and iii).

In Experiment iv, where only ·02 gramme of secretion was injected intravenously, no intravascular clotting followed, and the condition of the blood after death was in remarkable contrast to Experiments ii and iii, for it failed to clot as rapidly as usual, twelve minutes elapsing before the onset of coagulation. These results would be almost unintelligible were they not, so far, absolutely analogous to some effects produced by the introduction of the venom of our Australian snakes which have been more fully discussed by one of us* elsewhere.

The next most striking general effect of the poison is the sudden and great fall in the pressure of the blood, which is so marked a

* C. J. Martin, *loc. cit.*

feature of the curves shown. This may be due either to weakening of the heart's action or to diminished peripheral resistance caused by a sudden paralysis of the whole vasomotor centres, or to both causes combined. We are strongly of opinion that the former is the principal cause, but as the data at our disposal do not prove this to be the case, it is useless to discuss it further.

The drowsiness and general depression which formed so prominent a feature in the recorded cases following wounds from the spurs, and was also seen in our first experiment, would result from this fall of blood pressure and the consequent diminution of blood supply to the nervous system. As in these cases the poison was injected under the skin, it would only reach the general circulation slowly, and the onset of the symptoms would be more gradual.

Our first experiment also shows the local irritant action following subcutaneous injection, which is marked by great œdema and tenderness.

The capillary hæmorrhages found in our other cases are another manifestation of this irritant action.

Altogether there appears to be a remarkable analogy between the venom of Australian snakes and the poison of the Platypus. This resemblance is indicated by the following tabular statement:—

(1) The poisons both owe their toxic properties to proteid constituents.

(2) They both markedly retard or prevent the coagulation of the blood when small doses are slowly introduced.

(3) They both cause intravascular clotting when injected intravenously in sufficient doses.

(4) They both cause an almost instantaneous drop in the pressure of the blood.

(5) They both cause capillary hæmorrhages and œdema when locally applied.

In the production of local œdema platypus poison appears to be much more powerful. Snake venom, on the other hand, is *five thousand times* as virulent as our preparation of platypus poison, and the above comparison only obtains between platypus poison and snake venom diluted to this extent.

At the conclusion of our survey of the literature of this subject, we pronounced the opinion that as far as the evidence adduced went, it presented a very strong case in favour of the contention that these glands, at any rate at some seasons, produce a poisonous secretion.

We venture to think that the results of our experiments have established the fact that the secretion is poisonous at some time of the year. Whether the animal is capable of discharging a secretion possessed of poisonous properties at all seasons of the year is not at present determined. Creighton* states definitely that the gland is subject to seasonal variations in size just as is the case with the mammary gland and testes (Bennett). We have been unable to find on what evidence Creighton makes this statement; but the differences in minute structure observed by us lend support to this view.

The idea naturally occurs to one that this apparatus, which is confined to the male sex, owes its peculiar development to the operation of sexual selection. That it is a weapon used by the males on one another when conflicting for the possession of the females, is an idea which would become extremely probable if it could be established that the gland is specially developed at or about the pairing season. This is a point which could be settled without difficulty provided specimens could be obtained in sufficient number at suitable periods of the year, say August and February.

Bennett found developing ova in the uterus as early as September, so that in all probability the animals pair during the latter part of August and earlier part of September.

That the secretion obtained by us from the glands of an animal killed in June proved actively poisonous, whilst that from an animal killed in April was innocuous, is interesting in this respect,

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* *Loc. cit.*

although June would indicate a somewhat early preparation for pairing. We cannot, however, place much stress on this isolated observation, as it is quite possible that the difference in development was due to quite other causes. In the meantime the biological significance of these extraordinary organs must remain an open question.

In conclusion we wish to express our thanks to our able assistant Mr. Robert Grant for his help with the experiments.

DESCRIPTION OF PLATES.

Plate XXVIII.

Dissection of left femoral gland and duct (nat. size drawing). The leg is strongly rotated outwards. The skin, panniculus carnosus, and deep fascia have been reflected. The position and anatomical relations of the gland, duct, and spur are shown.

a., M. gluteus max. ; *b.*, M. erector spinæ ; *c.*, M. latissimus dorsi ; *d.*, M. iliacus ; *e.*, M. gluteus min. ; *f.*, M. gluteus med. ; *g.*, M. rectus ; *h.*, M. flex. long. halluc. ; *i.*, M. tibialis post. ; *j.*, femoral gland ; 2, duct (leaving gland) ; 2′, duct (near base of spur) ; 3, spur.

Plate XXIX.

Transverse sections of gland (× 10).

Fig. 1.—Section of gland of animal killed June, 1894, showing dilated alveoli.

Fig. 2.—Section of gland of animal killed April, 1892, showing fibrous condition.

Fig. 3.—Section of duct (showing two channels.

a., Epithelium of duct.

Plate XXX.

Transverse section of marginal portions of gland.

Fig. 1.—Section of gland of animal killed June, 1894.

a., Coarsely granular large alveolar cell (flat nuclei); *b.*, fibrous tissue of stroma ; *c.*, fibrous tissue of capsule ; *d.*, muscular layer of capsule.

Fig. 2.—Section of gland of animal killed April, 1892.

a., Small alveolar cell (nuclei round); *b.*, fibrous tissue of stroma; *c.*, fibrous layer of capsule; *d.*, muscular layer of capsule; *ee.*, bloodvessels.

Plate XXXI.

First portion of tracing obtained in Experiment iv.

Above is the record of respiration in which the downstrokes represent inspiration and the upstrokes expiration. Underneath this, is the record of the blood pressure in the carotid artery. At the point * the injection was given as described in the text. The time occupied by the injection is represented by the raising of the signal line (*s*).